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Seasonal stages characterizing the annual cycle of an inshore pelagic system[1]

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The annual cycles of the major components of the Kiel Bight pelagic system are presented and discussed in a semi-schematic form. Four sequential stages characteristic of the growth season are identified on the basis of the imports (new nutrients) and exports (sedimenting particles) of the system in relation to its structure. In stage 1 (the spring bloom), most of the production is based on winter-accumulated hence new nutrients; pelagic heterotrophs are of minor importance, and large-scale sedimentation of phytoplankton and phytodetritus occurs. In stage 2 (herbivorous copepod maximum) there is some input of new nutrients from the sediment; zooplankton biomass build-up is massive and sedimentation is very low. In stage 3 (summer stratified community), biomass and production are fairly constant and high, and food-web structure is highly complex; production is based largely on regenerated nutrients and sedimentation is low. In stage 4 (autumn blooms), the pattern is very similar to stage 1 except that the new production is based on nutrients accumulated in stagnant bottom water over the summer.

It is shown that some problems associated with balancing annual budgetary models can only be resolved in the context of such seasonal stages in the structure of the system. We show that ratios such as new/regenerated production, production/sedimentation, production/grazing, metazooplankton/protozooplankton, etc., vary seasonally in recurring patterns and can therefore be considered as macroscopic system properties. The importance of this type of differential holistic approach to the study of pelagic systems is stressed.

Introduction

The annually recurring patterns of fluctuation of biomass of the pelagic community are characteristic of climatic zones and have been summarized on a very general level by Heinrich (1962). Viewed in greater detail, however, the seasonal cycles of the major planktonic components invariably deviate from the respective zonal schemes, particularly in coastal regions. Mostly, these deviations are related to local hydrography and topography which, together with climate, set the basic boundary conditions determining the seasonal cycle of the plankton. At the species level of resolution, attempts at accounting for observed patterns of change have not proved very successful because of the large number of factors that can lead to changes in species composition (Smayda, 1980). These factors, or environmental parameters, frequently differentiated into physical, chemical, and biological groups, obviously differ in their respective impacts on the system. Some determine the total carrying capacity of the system, others the components of the system, and yet others will 'merely' be of importance at the species level. Although this is a banal statement, it is surprising how little effort has been devoted so far towards developing some sort of rigorous scheme for classifying these factors according to the space and time scales at which they operate and the organizational level of the system where their impact is greatest.

A step in this direction was taken by Margalef (1978), who pointed out the major processes, peculiar to the pelagic systems, that shape the course of their development. Pelagic systems at large are constantly subject to loss of essential elements via sedimentation. This selective loss process can only be compensated by non-selective input of dissolved nutrients via displacement of the environment, i.e. water of the surface layer, accomplished, as a rule, by vertical mixing. Thus, replenishment of the nutrient pools involves renewal of the environment. The 'new' environment is nutrient-rich and turbulent, which are features apparently conducive to diatom growth. As the pools of essential elements circulating within the surface layer diminish, flagellates increasingly dominate the phytoplankton and the community structure changes. It follows that the rate of decline of these pools via sedimenting particles is

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a fundamental property of a pelagic system on the same hierarchical level as the input of new nutrients via vertical mixing.

Margalef (1978) accordingly proposed a simple classification scheme, applicable at a very general level and with turbulence and nutrient concentrations as variables, that accounts reasonably well for the observed patterns of appearance of diatoms, red tides, and smaller flagellates. Factors such as temperature, grazing, or intrinsic physiological ability are either parallelisms or subordinate to the above environmental variables. This scheme, however, is restricted to the phytoplankton and only partly accounts for the gamut of structural changes commonly undergone by the whole pelagic system of a given locality in the course of a year. Although many of these changes can be attributed to peculiarities of the system under consideration, the general patterns obtained from widely separated regions can be strikingly similar (Smayda, 1980). Extension of the above scheme to include more such overriding variables, hierarchically ordered, will provide more insight into the functioning of pelagic systems as a whole.

The authors (Platt *et al.*, 1981) of a recent concise review on the state of marine ecological theory, are convinced that 'work on the holistic properties of ecosystems will have to be accepted as one of the major activities of biological oceanography' before we gain the 'ability to make valid predictions about the working of marine ecosystems'. In any holistic appraisal of a system, one will first have to define its boundaries; next, identify inputs and outputs through these boundaries; and finally, relate this system throughput to the structure and rates of interaction between the components of the system. Such a rigorous treatment of pelagic ecosystems has rarely been attempted so far because of the many variables involved.

In this paper, a classification scheme to analyse the seasonal cycle of a coastal pelagic system with an aim to defining some of its macroscopical properties is presented. The data base for this case study was collected over a period of ten years in Kiel Bight and includes several annual cycles of phytoplankton and zooplankton biomass and composition, nutrient concentrations, and sedimentation rates with a resolution of several days to two weeks. The most complete data set, including primary production, was obtained during 1973 and again in the first half of 1980. In the intervening period, information was collected at much shorter time scales (daily, during the plankton tower experiments) but limited to restricted periods. Much of the above data has been published, but only specific aspects of the system have been dealt with in the individual papers, albeit in

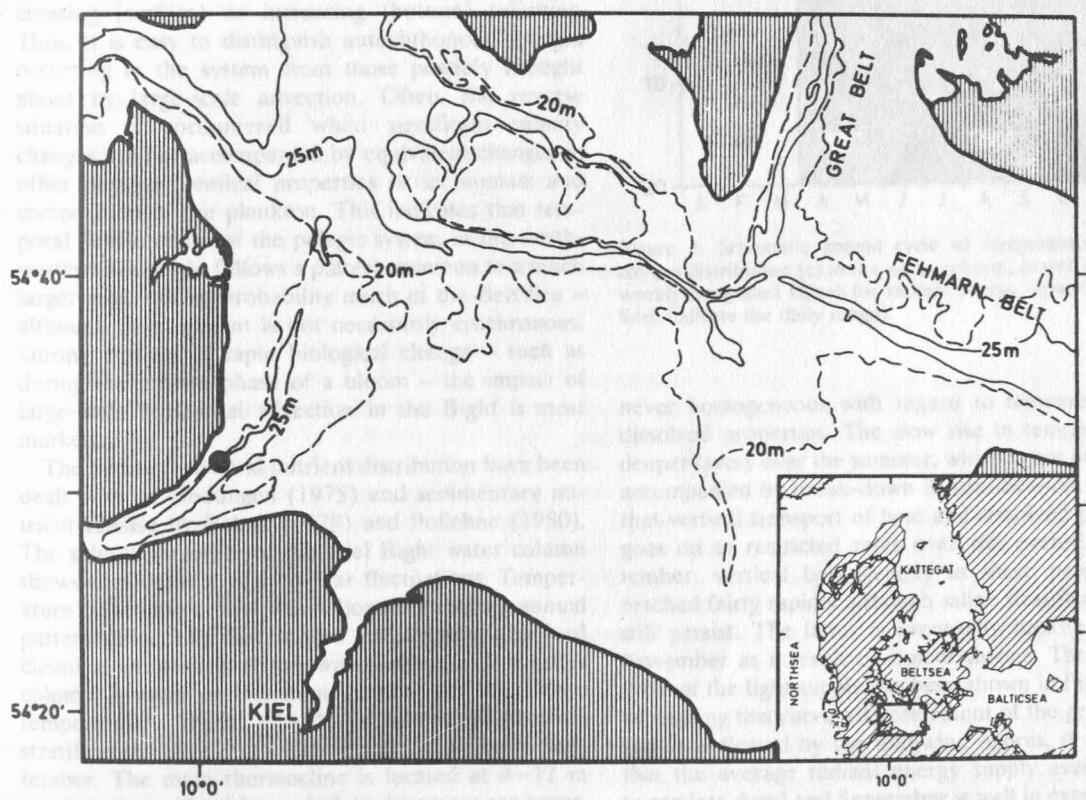

Figure 1. Location of the Kiel Bight in the Belt Sea, its topography, and the site of the routine station.

the light of whole system functioning. Here, we shall strive for a synthesis at a greater level of abstraction and shall therefore not go into the details of the actual observations. For the sake of clarity we have omitted what we feel is redundant or irrelevant and present the data in the form of schematic curves.

The Kiel Bight system

Physical and chemical environment

The location and general topography of Kiel Bight have been depicted in Figure 1. The average water depth of Kiel Bight is 17 m, and that of the euphotic zone approximately 15 m. The Bight is enclosed on all sides except for the northeast corner which is part of the main channel – the Great Belt/Fehmarn Belt – linking the North Sea with the Baltic. The study site, at 20 m water depth, is located in the opposite corner which is a dead end and where residence time of water is longer than in most other areas of the Belt Sea. The long-term average salinity of the water column in the southwest corner of Kiel Bight calculated from 18 years of observations is 18·7 ‰ (Babenerd, 1980) which is approximately a 1:1 mixture between Baltic (< 10 ‰) and Kattegat (~ 30 ‰) waters. Slight differences in the mixing ratio are clearly reflected in the salinity and any rapid major water exchange is immediately signalled by sharply decreasing (surface) or increasing (bottom) salinities. Thus, it is easy to distinguish autochthonous changes occurring in the system from those possibly brought about by large-scale advection. Often, the reverse situation is encountered when significant salinity changes are not accompanied by equivalent changes in other physico-chemical properties or in biomass and composition of the plankton. This indicates that temporal development of the pelagic system in the southwestern Kiel Bight follows a pattern common to a much larger area – in all probability much of the Belt Sea – although development is not necessarily synchronous. During periods of rapid biological change – such as during the growth phase of a bloom – the impact of large-scale horizontal advection in the Bight is most marked.

The hydrography and nutrient distribution have been dealt with by Bodungen (1975) and sedimentary nutrient release by Balzer (1978) and Pollehne (1980). The salinity structure of the Kiel Bight water column shows considerable year-to-year fluctuations. Temperature distribution, however, follows a recurring annual pattern (Fig. 2 a) that is also reflected in dissolved chemical properties of the water column. The water column is more or less homogeneous till May when temperatures reach 6°–8°C. Thereafter, thermal stratification develops which persists till about September. The main thermocline is located at 8–12 m depth and considerable vertical displacement can occur. The water column below the pycnocline in summer is

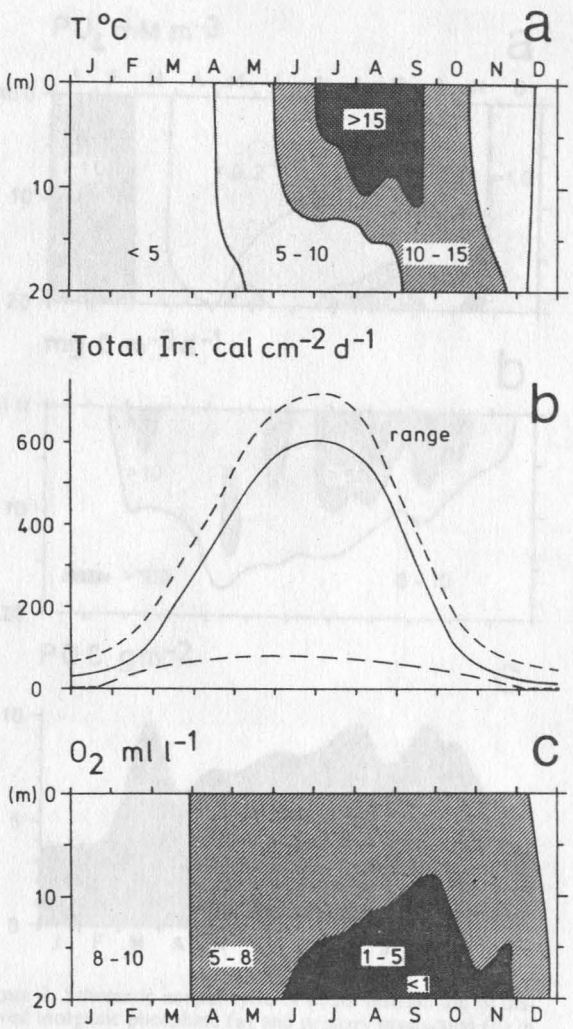

Figure 2. Schematic annual cycle of temperature (a) and oxygen distribution (c) in the water column, as well as average weekly integrated values for radiant energy input (b; dashed lines indicate the daily range).

never homogeneous with regard to temperature and dissolved properties. The slow rise in temperature of deeper layers over the summer, which is not necessarily accompanied by break-down in stratification, indicates that vertical transport of heat and dissolved properties goes on at restricted rates over this period. In September, vertical homogeneity in these properties is reached fairly rapidly although saline stratification may still persist. The latter is eventually broken down in November as a result of violent storms. The seasonal cycle of the light supply has been shown in Fig. 2 b. By comparing this curve with the extent of the growth season as indicated by the following figures, it is evident that the average radiant energy supply available between late April and September is well in excess of that required to build up phytoplankton blooms.

Vertical distribution of oxygen (Fig. 2 c) is homogeneous till June, after which depletion starts in deeper layers culminating regularly in anoxia in the deeper channel system (~ 25 m). The extent of anoxia varies and values < 1 ml l^{-1} are commonly found up to 18 m depth during August. Oxygen values in bottom water generally increase in September/October and there is a renewed phase of oxygen depletion in November. The water column is supersaturated only during the spring bloom and is generally slightly under-saturated, even within the upper 10 m, during most of the summer.

Nutrient distribution (Fig. 3 a) closely follows that of oxygen during the growth season. In winter, phosphate and nitrogen are remarkably constant (1·1 ± 0·1 µmol/l P and 12·1 ± 0·6 µmol/l N) and year-to-year variation is not observed. These are apparently equilibrium values, reached by the end of November, that are maintained by aerobic geochemical control at the sediment/water interface. Nutrient uptake by the growing spring phytoplankton bloom commences in late February, and nutrients are depleted in the entire water column when the biomass peak is reached. The annual nutrient minimum is always present immediately following bloom culmination. Thereafter, sporadic increases occur in bottom water, although continuous accumulation in this layer only starts after the onset of stable stratification. Vertical mixing in September/October introduces these accumulated nutrients to the surface layer.

Biological components and fluxes

Primary production and quantitative phytoplankton succession have been dealt with by Bodungen (1975), Smetacek (1975), Peinert *et al.* (1982), and Stegmann and Peinert (in press). The annual primary production of Kiel Bight is of the order of 125–175 g C m^{-2} yr^{-1}, more than half of which is regenerated production occurring during the summer. The production maximum in the water column is generally located well above 10 m, the only recurring exception being during the phase following the spring bloom when significant production occurs as deep as 15 m depth. The depth distribution, recorded during 1973, has been depicted in Figure 3 b. During spring and autumn, production is restricted to the surface although nutrient depletion occurs in the entire water column. Except for short periods, phytoplankton biomass is also fairly evenly distributed indicating continuous vertical mixing during these periods.

As the frequency of mixing declines during the late spring/early summer period, biomass tends to be less evenly distributed. During summer, phytoplankton populations, particularly large dinoflagellates, are distinctly layered. The growth season begins approximately nine weeks after the winter solstice but extends to six weeks before it. Light utilization by the autumn

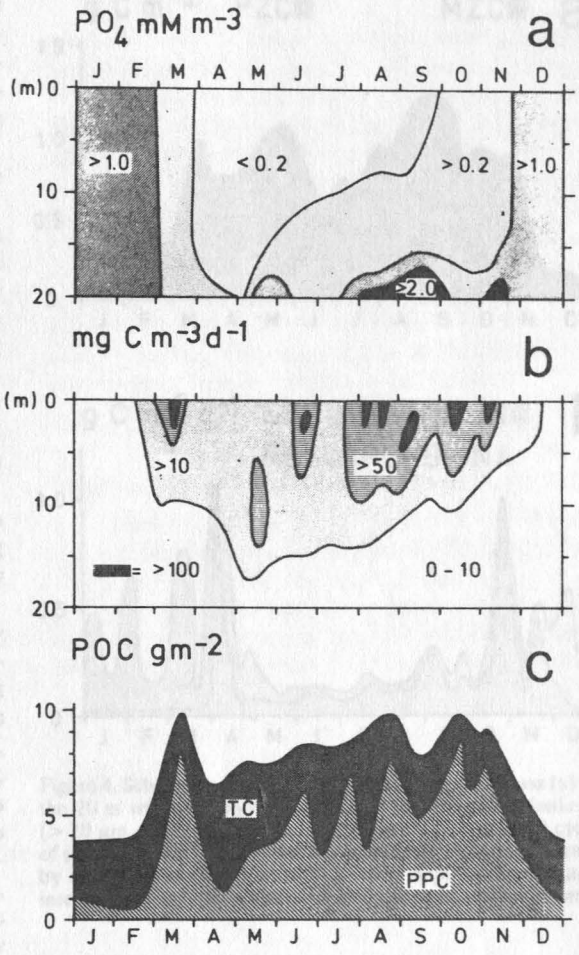

Figure 3. Schematic annual cycle of depth distribution of dissolved inorganic phosphate (a) and primary production (b) in the water column. Integrated values over the 20 m water column for particulate organic carbon (< 300 µm) subdivided into phytoplankton carbon (PPC) and particulate detrital carbon (tripton carbon = TC) are given in (c).

populations is hence much more efficient than by the spring ones (Bröckel, 1978), presumably favoured by autumnal and vernal differences in temperature as well as in the extent and intensity of short-term vertical mixing.

The nutrient sources of the phytoplankton vary considerably. During spring, the winter-accumulated pool is by far the major source as heterotrophic activity is low. This bloom is hence strictly 'new' production in the sense of Dugdale and Goering (1967). Following the demise of this diatom-dominated bloom (late March – early April), a population of small dinoflagellates invariably appears, which reaches its biomass maximum in May. Zooplankton biomass also increases, indicating that recycling within the pelagic system becomes increasingly important, although an input of new nutrient – from the sediments – must also occur to account for

the general increase in plankton biomass. The sedimentary input occurs fairly continuously and it appears that the motile, small-celled phytoplankton is specially adapted to exploit these conditions. The downward displacement of the production maximum towards the nutrient source is an indication of this adaptation.

During the summer, sedimentary nutrient input to the euphotic zone is restricted to the area above the pycnocline, and by far the bulk of the production can be attributed to regenerated nutrients released by the large pelagic heterotrophic population as well as the shallow benthos. As the latter suspension feeders are closely geared to the pelagic system, we regard nutrient input from this source to be regenerated and not new. Nutrients accumulated in pore water are, however, not part of the rapidly circulating pool, and their sporadic discharge into surface layers, as a result of density-driven sediment flushing, increases biomass (Smetacek *et al.*, 1982). The same applies to nutrients accumulated in deeper layers that are occasionally mixed up following storms or via horizontal displacement of surface layers resulting in restricted upwelling. Such inputs of nutrients accumulated over longer periods lead to new production and a resulting imbalance in the ratio phytoplankton–heterotrophs. A part of the new plant biomass is incorporated into the heterotrophic biomass and a part sinks out of the surface layer. In general, there is a steady increase in total plankton biomass, interspersed with peaks, over the summer months (Babenerd, 1980). Summer diatoms and dinoflagellates succeed each other or dominate the plankton over comparatively long periods (~ 4 weeks). In early autumn, input of nutrients accumulated in bottom water gives rise to the autumn blooms which are, as such, largely based on new production, as the role of pelagic heterotrophs decreases drastically.

The annual pattern of particulate organic carbon and phytoplankton carbon, described in detail by Smetacek and Hendrikson (1979), are depicted in Figure 3 c. Because of the constant nutrient concentrations available in spring, bloom size is similar each year. Greatest year-to-year variation occurs during the period after bloom demise because several independent factors – growth of the pelagic heterotrophic population, degree and frequency of vertical mixing, rate of sedimentary nutrient release – play regulatory roles. The summer levels are again more predictable as they are built up over longer periods. There is, however, great variation in the number and frequency of the biomass peaks generated by input of new nutrients since these are weather-dependent. The autumn dinoflagellate peak is again a constant feature in contrast to the last diatom bloom which occurs during rapidly deteriorating physical conditions. Water-column stability and sufficient light input during early November are prerequisites for this last bloom.

The seasonal cycle of zooplankton (Hillebrandt, 1972; Martens, 1976; Smetacek, 1981; Stegmann and

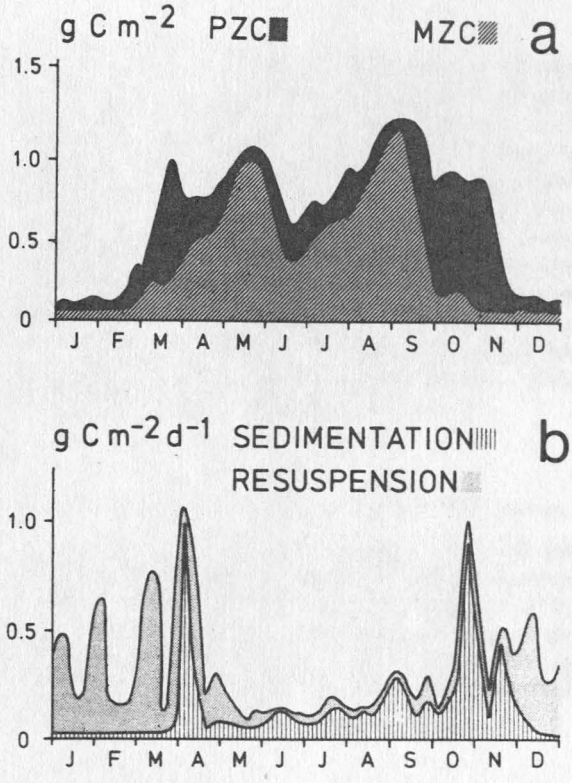

Figure 4. Schematic annual cycle of zooplankton biomass (a) of the 20 m water column differentiated into protozooplankton (> 20 µm, PZC) and metazooplankton (MZC). Annual cycle of sedimentation of particulate organic carbon (b) as collected by multisample sediment traps at 18 m depth, differentiated into primary sedimenting matter and resuspended sediment.

Peinert, in press) is much more predictable than that of phytoplankton, presumably because these organisms are less susceptible to the vagaries of the weather. In Figure 4 a, total zooplankton biomass, differentiated into phagotrophic protozooplankton and metazooplankton, have been depicted. The former dominate the bloom phases, whereas the latter are apparently geared to the regenerating phases. The first protozooplankton peak is a multiple one consisting of ciliates and dinoflagellates that feed both on the diatoms as well as on the succeeding flagellate populations. The first metazooplankton peak consists of a cohort of small herbivorous copepods that are spawned by overwintering adults during the spring bloom. This cohort apparently grazes heavily on the protozooplankton, which presumably subsists on material 'left behind' in the water column following bloom sedimentation. The flagellate population is subsequently heavily grazed by the growing copepod population.

After the decline of this first large cohort, for reasons not yet established, a new population builds up in summer. It comprises a mixture of species, with raptorial and filtering copepods being of equal importance, accompanied by large numbers of meroplanktonic larvae,

particularly those of mussels. Copelata and jelly-fish also contribute substantially to total biomass. The pelagic food web reaches its greatest complexity in summer and it becomes difficult to differentiate this community into trophic levels. Biomass of typical carnivores such as ctenophores and chaetognaths varies considerably from year-to-year, and it does not appear that these organisms exercise significant control over the zooplankton stock (Hillebrandt, 1972). The metazooplankton population declines rapidly in late summer for reasons not yet well known and takes only minor advantage of the autumn blooms. Protozoans again increase in importance, although they apparently also utilize only a small portion of this new production.

The fate of much of the organic matter produced during both spring and autumn blooms appears to be sedimentation rather than pelagic utilization. This is clearly seen from Fig. 4 b where the seasonal cycle of sedimentation, presented elsewhere by Smetacek (1980 b) and Peinert *et al.* (1982), has been depicted. Because of problems associated with separating resuspended sediment from freshly sedimented pelagic particles, as well as with catching efficiency of sediment traps, the absolute values of sedimentation are uncertain. Further, the contribution of zooplankton carcasses to sedimenting material is difficult to estimate. Nevertheless, the pattern of high sedimentation following the spring and autumn blooms as well as low sedimentation in the intervening period clearly reflects the general recurrent pattern. It is felt that these values are underestimates of the true vertical fluxes, although the seasonal pattern is in all probability valid. Approximately 30–60 g C m^{-2} yr^{-1} sediment out of the water column, of which two-thirds can be attributed to the spring and autumn blooms. This figure is also an indication of the magnitude of new production in the system.

Stages in the developmental cycle of the system

It is evident from the above account of the seasonal cycle of the Kiel Bight pelagic system that the observed changes are primarily the result of adjustment of the system to characteristics of the physical environment, although biological factors are also important. The relative importance of these factors in shaping the struc-

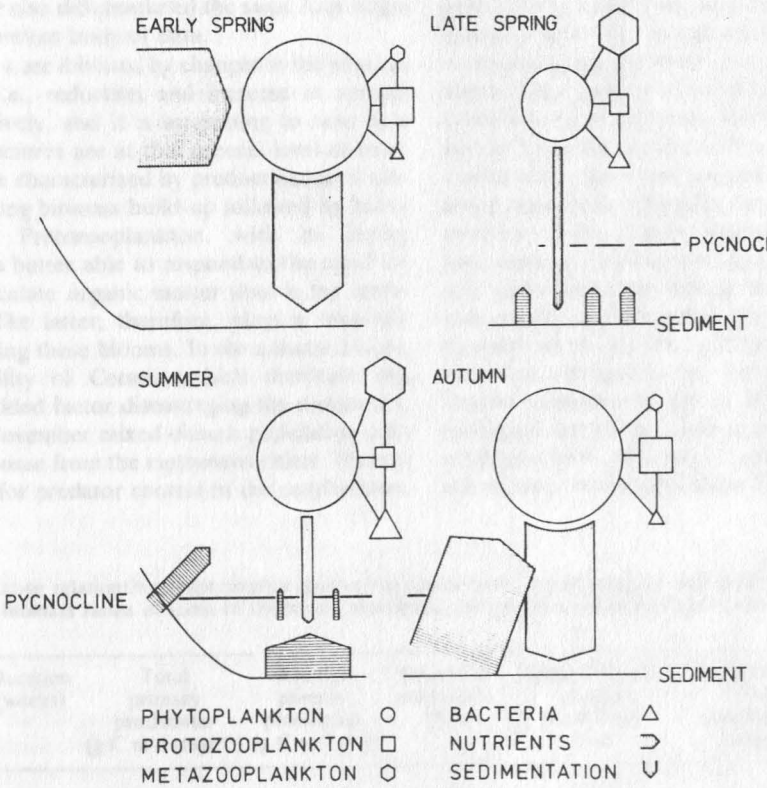

Figure 5. Semiquantitative flow diagrams representing the four stages of the pelagic system during the growth season. Arrows indicate input of new nutrients and output of sedimenting matter respectively. Quantitative relationships are denoted by the thickness of the arrows and size of the symbols representing the four major components of the system respectively. A detailed description is given in the text.

ture of the system varies over the year and it is possible to divide the seasonal cycle of the entire system into stages based on this criterion. The number of stages differentiated will depend on the degree of resolution sought. We have chosen to differentiate the growth season into four stages that have been depicted in the form of semiquantitative flow diagrams in Figure 5. Each model represents a particular stage.

In stage 1, the spring bloom model, the period between initiation and sedimentation of the bloom (5–6 weeks) has been integrated. The stage 2 model represents the 6–8 weeks following bloom sedimentation up to the decline of the first copepod maximum. The summer model (stage 3) does not integrate a longer time period but represents a typical 'day in the life' of the August system, i.e., in the absence of significant new nutrient input. The autumn model (stage 4) extends from the advent of vertical mixing to sedimentation of the bloom (4–8 weeks) and applies separately to both the dinoflagellate and the diatom bloom when there is one. Bacterial biomass and activity were unfortunately not recorded simultaneously with the other measurements. However, the seasonal differences indicated in these models are based on the results of microbiological research conducted elsewhere in Kiel Bight (Bölter, in press). Using non-parametric statistics and cluster analysis, Bölter also differentiated the same four stages from an independent body of data.

Stages 1 and 4 are initiated by changes in the physical environment, i.e., reduction and increase in vertical mixing respectively, and it is interesting to note how similar the structures are at this general level of resolution. Both are characterized by predominance of new production during biomass build-up followed by heavy sedimentation. Protozooplankton, with its higher growth rates, is better able to respond to the rapid increase in particulate organic matter than is the metazooplankton. The latter, therefore, plays a relatively minor role during these blooms. In the autumn bloom, the impalatability of Ceratia, which dominate this bloom, is an added factor discouraging the metazoans, although the November mixed diatom population does not elicit a response from the metazoans either. There is little evidence for predator control of the zooplankton. It is likely that internal cycles of the Kiel Bight metazoans are more important in regulating their appearance rather than the actual food supply.

Stage 2 is more than a mere transition stage between 1 and 3 since it has its own typical properties and characteristic populations geared to each other that culminate before the summer phase is established. Loss rates out of this system are amongst the lowest of the year, indicating this type of pelagic structure to have a great retention capacity. The quantitative relationship between phytoplankton and zooplankton is apparently the crucial factor rather than species composition (Smetacek, 1980 a). Wastes produced by the latter as faecal pellets are recycled quantitatively, coprophagy by the copepods (Paffenhöfer and Knowles, 1979) presumably being the decisive mechanism here. New nutrients entering the system are rapidly passed to the zooplankton; its biomass peak is surprisingly constant each year and apparently independent of phytoplankton, which has a biomass that varies much more. The copepod maximum of stage 2 is as recurrent a feature of the annual cycle as is the spring bloom of the preceding weeks, although the latter is a food source only for spawning females and the youngest stages of the former.

Stage 3 is the antithesis to the bloom stages as it represents a steady-state phase. Both input and output rates of this system are small in comparison with the turnover within it. The autotrophic and heterotrophic components are intimately geared to one another, presumably in a fashion whereby loss of essential elements is reduced to a minimum. Particles sinking out in this period have the highest C/N and C/P ratios ever recorded from the water column (Pollehne, 1980), and being apparently refractory they truly represent 'waste products' of the system. Because of continuous, albeit low, input of new nutrients from flushing of sediments and from restricted mixing at the thermocline, that compensate losses to sedimentation, comparatively high biomass levels can be maintained over long periods. However, changes in the species composition of the various components are in all likelihood driven by biological factors not evident at the level of resolution addressed here. The many feeding types represented in the summer metazooplankton (Schnack, 1982) indicate

Table 1. Quantitative relationships expressed as approximations between inputs, outputs, and production within the system as well as range in biomass ratios of some of the major planktonic compartments characteristic of the four stages of the growth season.

Stage	Duration (weeks)	Total primary production (g C m^{-2} $stage^{-1}$)	Average primary production (g C m^{-2} d^{-1})	New total production (%)	Sedimentation of total production (%)	Phytoplankton: total zooplankton biomass	Metazooplankton: protozooplankton biomass
1	6–8	~ 20	0·4	> 75	> 50	> 10	0·3–0·1
2	6–8	~ 20	0·4	~ 50	< 25	3–1	5–0·3
3	12–14	~ 70	0·8	< 25	< 25	6–3	2–5
4	6–8	~ 30	0·6	> 75	>75	> 10	1–0·3

that apparently all the size classes and groups of phytoplankton and protozooplankton are indeed utilized. An important exception are the Ceratia that steadily build up their biomass in the course of the summer. The summer Ceratia are distinct from the autumn population, and it appears that the former also sediment out of the system at the end of the summer.

However, not enough is known about the mechanisms involved to differentiate a transition stage between stages 3 and 4 at present. More detailed study of the biological mechanisms involved in determining the components of the system will be necessary before additional stages, such as the red tides that occur in some years, can be identified and defined.

The characteristic quantitative features of the four stages outlined above have been presented in Table 1. The ratios listed in this table are what we consider to be some of the macroscopic properties of the system. Needless to say, these figures are highly generalized; some have been actually measured, others are indirect estimates. They summarize the relationship between import, patterns of utilization, and export of the various systems. Additional ratios not included because of incomplete data, such as phagotroph–osmotroph biomass, are also likely to provide useful insight into the functioning of particular systems. Subdivision of the components listed here into categories pertaining to size, motility, and palatability of the phytoplankton, feeding mode, reproduction mode, and the herbivore–carnivore ratio of the zooplankton, etc., would permit characterization of the various systems at a more detailed hierarchical level than the one presented here.

Discussion

Four characteristic stages of the pelagic growth season in Kiel Bight have been differentiated here. They are recurrent features of the annual pattern, since this sequential cycle is driven by forces generated by the interaction of topography, climate, and geochemistry of the region as well as by the inherent properties of plankton biology. However, the onset and duration of each stage as well as the species composition of particularly the phytoplankton can vary from year to year. Comparative analyses of cycles from similar regions will greatly further our understanding of pelagic systems and their coupling to the relevant physical environment. It is essential, however, that compatible hierarchical levels be compared with one another in terms of the features outlined above. Interregional comparisons of species succession within individual components of pelagic systems, carried out in the past (Smayda, 1980), have generally contributed little towards clarification of the underlying driving forces.

Quantitative structural changes in a pelagic system over an annual cycle were first recorded by Lohmann (1908), although the question of the forcing functions driving these changes gave rise to much dispute in the following years (Brandt, 1917). Since then, a host of new issues have arisen, particularly related to quantitative aspects of interaction within the system, and now, some of the widely accepted views have come under attack. For instance, the assumption that the first annual zooplankton maximum is geared directly to the spring diatom bloom has been disproved for Kiel Bight. Fransz and Gieskes (1984) have shown that this does not apply to the North Sea as well. The underlying belief that all of the phytoplankton is consumed by zooplankton evidently needs to be re-examined. What then is the fate of the non-eaten phytoplankton?

Sedimentation of a substantial portion of the spring bloom has been reported, either based on direct observations or indirect conclusions, from other areas, such as a lake (Jewson *et al.*, 1981), a Norwegian fjord (Skjoldal and Lännergren, 1978), a bay (Platt and Subba Rao, 1970), and a coastal shelf (Coachman and Walsh, 1981). It is likely that sedimentation of phytoplankton is always a significant process in eliminating plant biomass from the surface layer, following blooms based on new production that are terminated by nutrient exhaustion (Smetacek, in press). Only in regions where plant biomass build-up is rivalled by that of metazoans, will a correspondingly larger portion of the new organic matter be retained within the pelagic system. Mass sedimentation of Ceratia blooms has also been reported from other areas (Mahoney and Steimle, 1979).

Other disputed or simply open issues are those pertaining to the relative roles of physical and biological factors in shaping the structure of pelagic ecosystems, the role of various heterotrophic compartments in total community respiration, the relationship between assimilation efficiency of individual organisms and ecological efficiency between trophic levels, the magnitudes of production of the various trophic levels, etc. As shown by the analysis of the Kiel Bight system, none of these issues can be satisfactorily explained by simple answers but have to be regarded in the relative context of structure and functioning of a particular type of system or stage.

The scheme for classifying the annual cycle of a given region presented here is by no means innovative. The spring, summer, and autumn periods are clearly differentiated in the diagram of the seasonal cycle representing the North Atlantic by Heinrich (1962). A heterotrophic phase succeeding the autotrophic spring bloom phase was differentiated by Sorokin (1977) for the Japan Sea. Further, the basically different mode of functioning of bloom and steady-state phases that succeed each other was described by Yentsch *et al.* (1977), who compared the former with a 'boom-and-bust' type economy and the latter with a recycling one. Parsons (1976) also discussed the reasons underlying widely divergent community structures encountered by different

workers in the same region (off the Peruvian coast) and season but in different years.

However, there have been few attempts to reconcile some of the contemporary controversies in terms of the seasonal development inherent to the structure of pelagic systems. The biggest problems have emerged in the field of quantitative annual budgets of given regions (e.g., Steele, 1974; Mills, 1980). Such budgets, based on annual figures of primary production and direct and indirect estimates of production in the following trophic levels, are generally faced by a serious food shortage; i.e. apparently not enough is produced in the system to satisfy the demands of its heterotrophic components (Platt *et al.*, 1981). On the other hand, Walsh (1981) has presented evidence indicating that the shelf regions of the world (where the majority of budgets have been made) are a major global depositional site of carbon that is buried as organic matter. The implication here is that production significantly exceeds remineralization in shelf regions.

Apparently, our concepts of the quantitative aspects of pelagic system functioning are faulty at a very fundamental level and further attempts at formulating quantitative models of pelagic communities averaged over the year will not help (Mills *et al.*, 1984). Nor will generalizations, aimed at the pelagic community at large, help if they are merely based on observation of a particular stage, no matter how detailed the data. The overall system context, defined by its macroscopic properties, will now have to be taken more explicitly into consideration (Platt *et al.*, 1981). Thus, rather than attempting to find generally valid solutions for some of the issues mentioned above, one should regard them as variables and hence as a basis for defining the properties of the system. We need to approach the study of pelagic ecosystems at different hierarchical levels defining them in terms of their properties as we progress from the general to the particular. Such a classification scheme would be analogous to the forest, grassland, desert classification with further hierarchical subdivisions of terrestrial ecology. In pelagic systems, however, spatial zones as well as temporal stages have to be differentiated. Development of classification schemes of pelagic systems according to successive sets of their macroscopic properties will do much to improve our understanding of the workings of these systems as each such scheme will provide the necessary context in which data from various regions and seasons can be compared. This paper is intended as a step in this direction.

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Sedimentation of planktonic diatoms in the Antarctic: Evidence of a mechanism for accelerating sinking rates

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Abstract. A mechanism for accelerating sinking rate by compaction of chains into clumps in the common phytoplankton genus Thalassiosira is described. The clumps, previously regarded as fecal pellets, generally contain resting spores. Settling out in shallower water ensures retention of a seeding population there and diminishes loss to the deep ocean. Because of the large biomass involved, this seeding strategy can have important implications for oceanic biology and geology.

A few genera of marine planktonic diatoms - the so-called bloom diatoms (1) - dominate organic production in the fertile regions of the sea. Sedimentation of bloom diatom biomass fuels the major demersal fisheries and its burial in shelf and slope sediments may significantly affect global carbon and nitrogen cycles (2). Zooplankton fecal pellets are believed to mediate sedimentation (3, 4) since reported sinking rates of phytoplankton cells are too small to account for the apparent rapidity of vertical flux (5). However, evidence now accumulating indicates that direct sedimentation of phytoplankton can be significant (2, 6, 7), although the causes and mechanisms of rapid bloom sinking are obscure. Nutrient depletion following water column stratification is assumed to trigger the sedimentation process which is generally equated simply with mass mortality (2).

Here we report sedimentation of bloom diatoms (Thalassiosira sp.) from turbulent, nutrient-rich Antarctic waters. Cell sinking rates are accelerated by resting spore formation and by compaction of loose chains into gelatinous clumps. These clumps apparently represent seeding stages in algal life history. Our findings provide the first observational support for the hypotheses argued elsewhere (8) that rapid sinking of diatom blooms represents a seeding strategy and is effected by the algae themselves.

The investigation was carried out in the northwestern opening of the Bransfield Strait, between the South Shetland Islands and the tip of the Antarctic peninsula, during November/December 1980. Spatial distribution of phytoplankton and zooplankton biomass and species composition in relation to environmental variables was monitored with standard methods (9). Sedimentation rates were measured on 6 occasions with free-drifting sediment traps (10) located at 100 m depth. Trap material was immediately examined under a microscope. Aliquots were utilized for chemical analyses and a portion was preserved with formaldehyde and later examined in greater detail.

Distinct hydrographical zones with diatom blooms in different growth stages were found, despite consistently high ambient nutrients. Zooplankton biomass was small throughout (9). A vigorously growing Thalassiosira population was present in stratified water on the northern shelf and the central Bransfield Strait. On the southern shelf, the vertically homogeneous water column indicated ongoing intense mixing down to the bottom (ranging to 400m depth). The large phytoplankton biomass (also Thalassiosira spp.) in this zone must have developed under previously stratified conditions and was now undergoing resting spore formation throughout the water column. The population appeared to be stressed by light reduction due to deep vertical mixing.

Significant differences in quantity and composition of trap material were found in the 2 zones. Krill feces (11) dominated collections in the

stratified zone and were responsible for quantitative variations (0.1 - 0.5 g C m^{-2} d^{-1}) amongst the 3 traps deployed here. Surprisingly, extensive trawling for krill yielded only meagre catches. Intact phytoplankton cells and spores comprised up to 20% of trap material in this zone. On the southern shelf, zooplankton feces were rare and trap material consisted mainly of long Thalassiosira chains (up to 150 cells) with resting spores. The larger collections in the mixed zone (0.5 - 1.4 g C m^{-2} d^{-1}) were partly due to the traps' location within the phytoplankton population rather than below it. However, the proportion of resting spores to vegetative cells was much higher (factor of 4) in trap material than in water column samples indicating that traps selectively accumulated particles with higher sinking rates (12). Diatom spores sink more rapidly than vegetative cells (13).

All 6 traps collected significant numbers of compact clumps that were tightly packed with up to 150 Thalassiosira frustules. Clumps ranged in size from 100 - 200 µm and were initially mistaken for zooplankton feces; subsequent closer examination revealed that they consisted of tightly rolled chains always with intact frustules (Fig. 1).

The compact clumps were only encountered in trap material. However, since various stages of the formation of such clumps from chains of vegetative cells were common in water column samples from the southern shelf, reconstruction of the process from preserved material was possible. The stiff, chitan (similar to chitin) bristles that radiate out from the frustule rim in vegetative cells (Fig. 2A) play an important role in clump formation. In the initial stages, the bristles of one cell appear to become sticky and then keel over like a closing umbrella and adhere to those of the adjacent cell. Sequential "umbrella closing" results in enclosure of the chains within a loose gelatinous envelope supported by the bristles (Fig. 2A,B). This envelope later contracts into a tight gelatinous skin over the compacted cells of the chain (Fig. 2C). In this stage, the bristles apparently soften and collapse against

the chain, possibly due to release of enzymes by the cells. The gelatinous covering of these chains appears to be a sticky mucus secreted by the cells which can cause incorporation of other particles into the clumps. In one case, a deformed but intact cell of the diatom Corethron , which has extremely long and fragile silica spines, was found wrapped into a Thalassiosira clump (Fig. 2D). Presumably, the Corethron cell initially adhered to a gelatinous chain and then was 'dragged' gently into the clump by subsequent contraction. Various stages of the formation of compact clumps (Fig. 1; 2D,E) by entwinement of gelatinized chains (Fig. 2A,B,F) were found. Possibly, other chains were also captured during this process.

Gelatinization of chains was generally accompanied by resting spore formation (Fig. 2 C,F), although vegetative cells were also found in clumps (Fig. 2D,E). Lumps of shrivelled plasma were commonly observed in gelatinized chains (Fig. 2A,B) that apparently represented aborted resting spores. This we conclude from examination of over 500 gelatinized chains with various stages of resting spore formation and abortion. Insufficient cellular reserves and/or their exhaustion during mucus production were presumably the reason for abortion (14). Gelatinized chains with shrivelled plasma had low sinking rates as they were common in the water column but conspicuously absent from trap collections (unless associated with clumps).

Such an elaborate mechanism of clump formation from chains strongly suggests that it has survival value; however, the relationship between form and function in marine phytoplankton is basically unresolved (15). The current paradigm in marine ecology implicitly assumes that phytoplankton biomass in the surface layer is controlled solely by growth and grazing (16); life history strategies of the algae involving significant movement within the environment are rarely considered. Thus, phytoplankton form is generally regarded either in relation to requirements of the growth environment or to

herbivore deterrance. Expansion of the current paradigm to include environmental selection of algal seeding strategies can well add a new dimension to our understanding of phytoplankton ecology. This subject has been discussed at length elsewhere (8); here we argue, for the following reasons, that clump formation by Thalassiosira is part of a seeding strategy effecting maintenance of a benthic seed population in shallow regions: 1) deterioration of the growth environment, in this case reduction in light supply, triggers both resting spore and clump formation; 2) the high sinking rates will eventually result in deposition on the bottom; 3) the sticky clumps will serve to anchor cells to the sea bed, an important requirement for benthic spores in turbulent water; 4) benthic resting spores are a wide-spread feature of coastal marine phytoplankton (8); 5) herbivore deterrance is a more acute requirement for seeding than for vegetative stages particularly in an animal-rich environment such as the benthos. Further, encapsulation might prevent leakage of chemical cues to herbivores such as krill in which feeding is triggered by dissolved substances in the environment (17).

In regions with extreme seasonality, such as the Antarctic, phytoplankton will have to perforce undergo a period of dormancy, whether suspended in the water column, attached to surface ice or lying on the bottom. Coastal diatom blooms in other regions form resting spores on nutrient depletion following seasonal stratification (8, 13). In the Antarctic, stratification is transient and nutrients, therefore, always abundant; thus, other factors, e.g. light deprival following deep mixing, must serve as the triggering factor for resting spore formation (18). In the absence of a triggering factor, blooms developing in the productive shelf areas would be eventually advected and dispersed in deep circumpolar waters. Concomitant clump and spore formation by individual chains would ensure deposition of a seeding population on the shelves in spite of a highly turbulent water column. Mortality will be high in such a seeding strategy as populations advected out of the shelf regions will

"loose" their spores to the deep sea. However, the entire population is not deposited on the sea floor since the shorter chains will be retained by turbulence within the water column. Thus, there will be both benthic as well as pelagic seeding stages - the former ensuring regional persistence and the latter dispersal. Bloom diatoms in general are likely to follow both strategies and species-specific differences in this behavior can well be selected for by local topography and hydrography (8).

We have also observed clump formation in various Thalassiosira spp. from the Baltic, the Norwegian Sea and the open North Atlantic but not yet in a magnitude comparable to that found in the Antarctic. Presumably, cell aggregation is a wide-spread phenomenon in diatoms with chitan bristles that has been overlooked so far for 2 reasons: 1) the residence time of clumps in the water column is short because of their high sinking rates; 2) such clumps are intuitively classed as zooplankton fecal pellets. For example, the "copepod fecal pellets" described by Schrader (3, 19) from the Baltic are in all likelihood such diatom clumps. A clump of Achnanthes taeniata, a ribbon-chained, pennate diatom from the Baltic, has been depicted in Fig. 3A which is identical to the objects identified as fecal pellets by Schrader (19). For comparison, a copepod fecal pellet collected in the same water column as the Achnanthes clump is shown in Fig. 3B. The difference is obvious, and even though intact diatom cells are common in copepod pellets, the arrangement of frustules in the clumps cannot be attributed to zooplankton handling.

The geological implications of concomitant mucus secretion and rapid sinking of diatom blooms are considerable (8). Zooplankton feces including those of krill are not considered important in formation of diatomaceous ooze in the deep sediments of the study site (20). Krill feces rarely contain intact frustules (Fig. 3C) which, however, figure prominently in the ooze. Further, disintegration of the fragile krill feces apparently occurs within

the upper 1 000 m (20). Possibly, clumps and loose aggregates of sticky chains will be responsible for much of the downward transport of frustules. Schrader's (3, 19) observations from the Baltic also indicate that diatom clumps have high sinking rates; further, the gelatinous covering appears to protect the frustules from dissolution (3, 19). Similar clumps with high sinking rates have also been reported from coccolithophore species (5, 21) where they presumably also represent a seeding strategy (8). Gelatinous clumps can scavenge other suspended particles which, if mineral, greatly accelerate sinking rates. This mechanism would explain the rapidity of vertical flux following diatom and coccolithophorid blooms and also the observed synchronicity of biogenic and mineral particle input to the deep sea (21, 22, 23).

Figure legends

Fig. 1. A. Unpreserved trap material from the stratified zone (Antarctic peninsula shelf) showing a zooplankton feces (1), a short Thalassiosira chain (2) and a compact clump (3). Note resting spores in clump and chains.

B. Scanning electron micrograph of a Thalssiosira clump. The "skin" is dried mucus. Note pennate diatom (center) and sundry particles (lower half) incorporated into the clump.

The bar (upper right) is 50 µm.

Fig. 2. Various stages of clump formation by Thalassiosira chains from preserved water samples (Antarctic peninsula shelf) (A, B, C). The loose envelope supported by chitan bristles is prominent in A and B, and has compacted in C. The stiff chitan bristles of vegetative cells (on the left in A and C) can be discerned.

Compact clumps from sediment traps (Antarctic peninsula shelf) (D. E, F); a Corethron cell incorporated into a clump (D); a compact clump (E) and a loose clump (F).

Note shrivelled plasma in A, B, resting spores in C, F and vegetative cells in D, E. The bar (upper right) is 50 µm.

Fig. 3. Scanning electron micrographs showing a clump of the pennate diatom Achnanthes taeniata (A) from the Baltic, a partially decomposed copepod fecal pellet (Pseudocalanus elongatus) (B) from the same water column as (A) and the amorphous contents of Antarctic krill feces (C). The bar (upper right) is 50 µm.

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12. Traps suspended in turbulent water do not collect material by simple passive sinking. Rather, turbulent mixing results in constant water exchange with the environment and only those particles that successively sink through zones of declining turbulence within the trap eventually accumulate in the dead zone of the collection glass.Thus, traps select particles with higher sinking speed.

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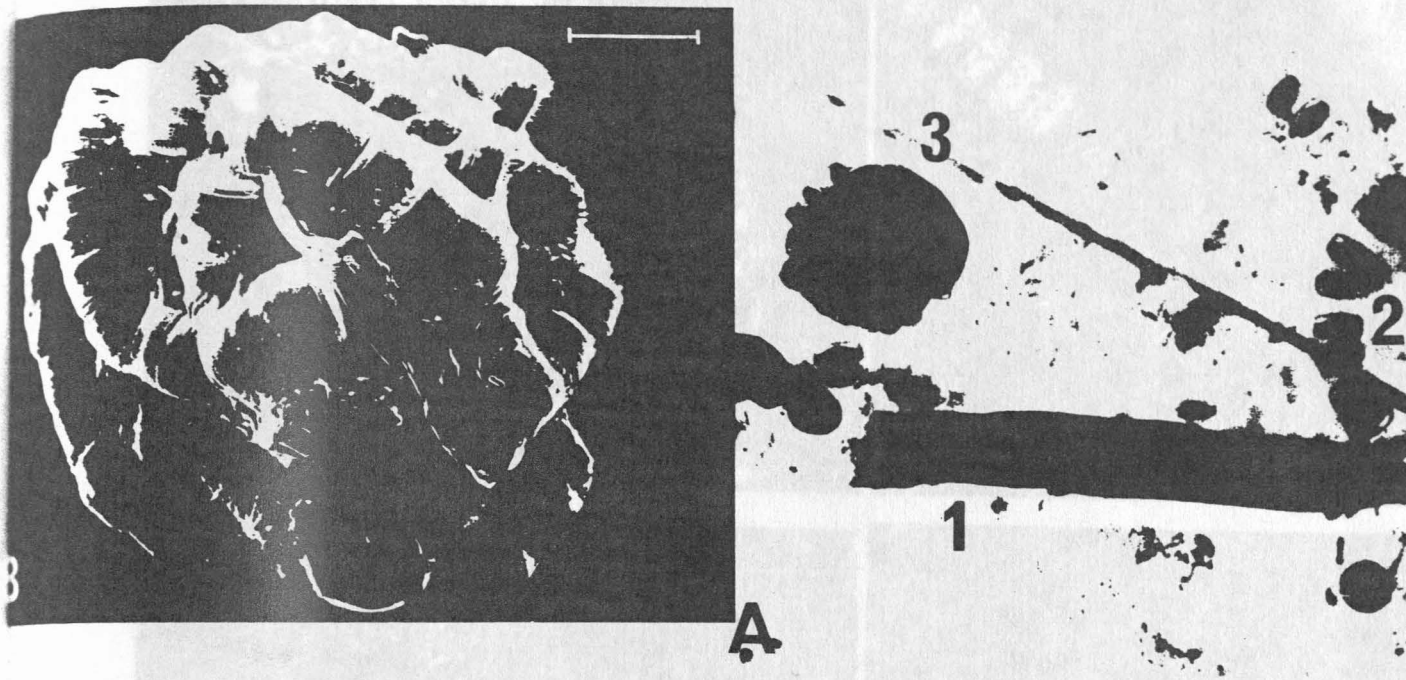
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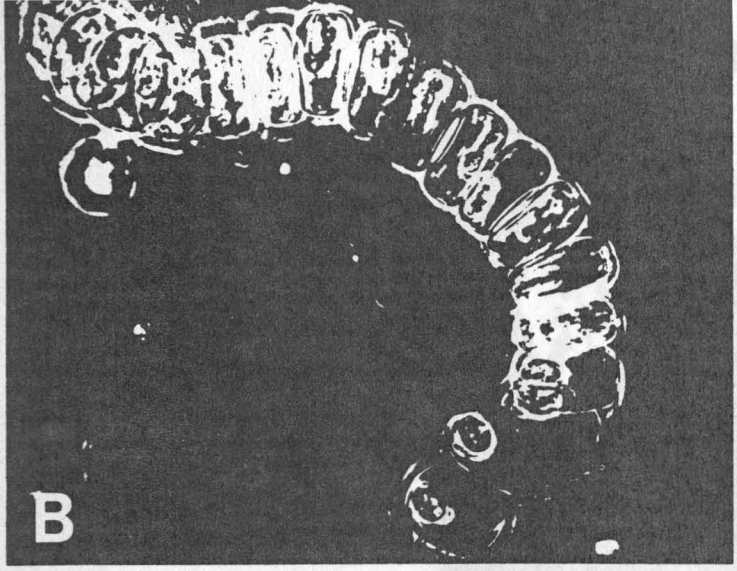
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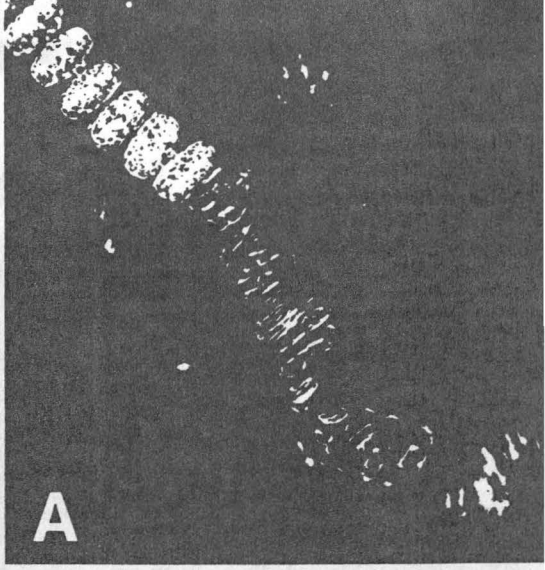
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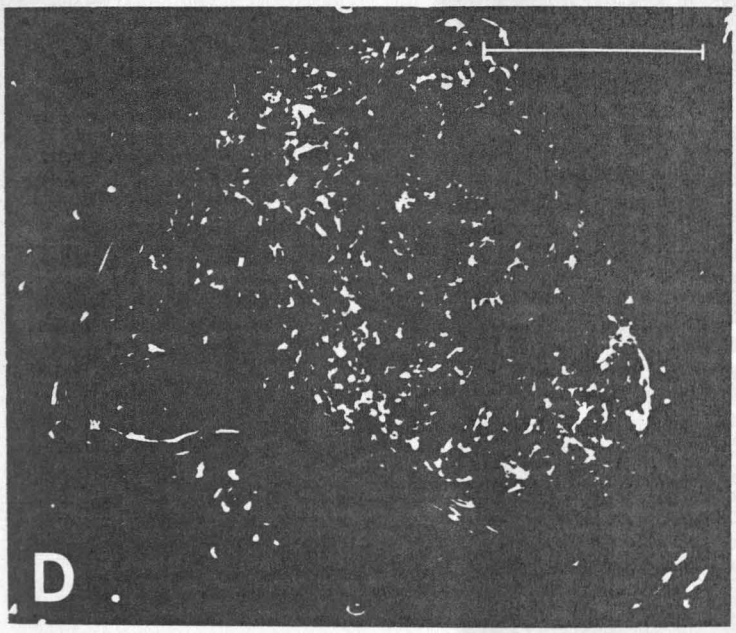
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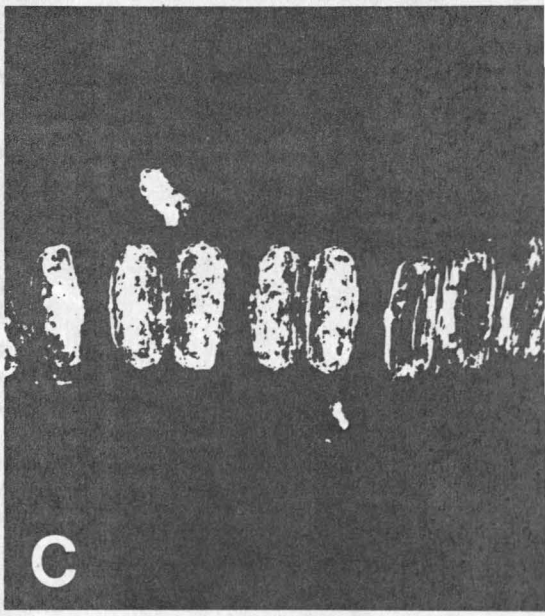
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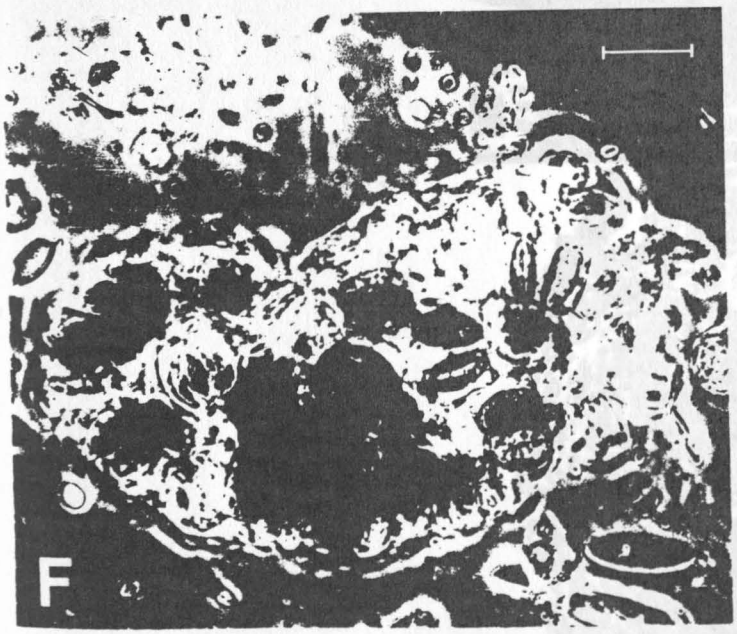
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